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REPRODUCTION OF THE MARSH HARRIER *CIRCUS AERUGINOSUS* IN RECENT LAND RECLAMATIONS IN THE NETHERLANDS

C. DIJKSTRA^{1,2} & M. ZIJLSTRA¹



Dijkstra C. & M. Zijlstra 1997. Reproduction of the Marsh Harrier *Circus aeruginosus* in recent land reclamations in The Netherlands. *Ardea* 85: 37-50.

We studied temporal variation in reproductive performance of Marsh Harriers *Circus aeruginosus* in two land reclamations in The Netherlands, i.e. South Flevoland and the Lauwersmeerpolder, embanked in 1968 and 1969 respectively. The number of breeding pairs in Flevoland rapidly increased to a maximum of 350 pairs (± 1 pair km⁻²) in 1977, followed by a sharp decline in the 1980s due to large-scale cultivation. The same trend was observed in the Lauwersmeer, although colonization was retarded and peak densities were reached later. In both study areas mean clutch size as well as the number of fledglings per nest decreased in the course of the twenty years of study. Two factors were responsible for this decline in reproductive output: (1) decrease of food abundance in the course of the years, and (2) an increase of nest predation, mainly by the Red Fox *Vulpes vulpes*. Superimposed on these long-term changes, annual fluctuations in density of the Common Vole *Microtus arvalis* had a considerable effect on the number of breeding pairs, as well as the fledgling production. Mean annual clutch size was associated positively, and laying date negatively, with the average annual temperature during the pre-laying phase.

Our results indicate that the early stages of succession, during the first decade after reclamation, are characterized by high prey abundance (i.e. vole 'plagues') and low densities of ground predators, and offer favorable breeding conditions for Marsh Harriers. The simultaneous negative effects in recent years of less breeding habitat, decreased prey abundance and increased predation on reproductive output, exert pressure on these populations. The intense nest predation (50% of all nests), as recorded in the Lauwersmeer since 1990, may eventually cause local extinction in the absence of, relatively safe, inundated breeding habitat.

Key words: *Circus aeruginosus* - reproduction - succession - predation - prey abundance - *Vulpes vulpes* - *Microtus arvalis*

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INTRODUCTION

The past three decades have witnessed substantial increases in numbers of many raptor species in W. Europe. These changes are probably attributable

to the ban on organochlorine pesticides and laws against persecution (Bijleveld 1974, Newton 1979). For some raptor populations in The Netherlands, there has simultaneously been a third factor of potential importance: several large scale land



reclamations in the 1960s. In earlier reclamations, e.g., in the Noordoostpolder, a 490 km² polder reclaimed in 1940, it was noted that especially the Marsh Harrier *Circus aeruginosus* bred in high densities for a number of years (Bakker 1954). Cultivation of the land caused this to be only a temporary settlement. With the creation of the polders 'South Flevoland' (1968) and 'Lauwersmeer' (1969), it was decided to monitor raptor populations more closely, and study their responses to the changes in habitat. Because of rapid succession and change in land use, the polders provided a unique opportunity to study the responses of different bird species. In particular, to assess the extent to which marked population fluctuations are attributable to, on the one hand, changes in reproductive output, and on the other to numerical responses of the adult population in terms of dispersal and survival. In the present paper, we evaluate thirteen years of data on reproduction of the Marsh Harrier in Flevoland, and eighteen years of data from the Lauwersmeer area.

The Marsh Harrier lends itself in particular to this analysis, since it is a bird adapted to breeding in high reed *Phragmites australis* vegetation, characteristic of young polders. Marsh Harrier reproductive biology has been intensively studied in more stable marshlands in Poland (Witkowski 1989) and France (Bavoux *et al.* 1989), and these data will be used as a reference in our current analysis. The conspicuous increase of the breeding population in the Lauwersmeer has been reported by Altenburg *et al.* (1987). In addition to reproductive parameters, we have collected and analysed data on one of the primary food items, the Common Vole *Microtus arvalis* and on a dominant predator, the Red Fox *Vulpes vulpes*. It is well known that one of the typical changes following embankment of new polders is a temporary outbreak of voles (Noordoostpolder: Bakker & van der Zweep 1949; East Flevoland: Cavé 1968; Lauwersmeer: Timmerman 1971; Volkerak: Dijkstra 1994). This may well be an influential factor in fluctuations of raptor populations. Predators (and food competitors) such as the Red Fox

colonize the new areas more slowly. It is thus of interest to evaluate how these biotic factors have affected reproductive rates in the Marsh Harrier.

STUDY AREAS AND METHODS

Data on Marsh Harrier reproduction were collected in two polders in The Netherlands: South Flevoland (52°20'N, 05°20'E; 430 km²) was reclaimed from the fresh water lake IJsselmeer in 1968, and the Lauwersmeerpolder (53°20'N, 06°15'E; 91 km²) in 1969 from the Waddensea. In South Flevoland, reed was sown for soil-ripening purposes in the year after embankment, resulting in extensive suitable breeding habitat for Marsh Harriers in 1970. During the following fifteen years the polder was gradually brought into cultivation, except for c. 40 km², (i.e. 9% of the total area) in the nature reserves Oostvaardersplassen and Lepelaarplassen (Fig. 1). During the first 5-10 years of cultivation, extensive state-managed agriculture was carried out, before the ground was sold for private, intensive farming. Eventually 53% (230 km²) of the polder was transformed into agricultural land, and 21% (90 km²) was forested. Another 17% (70 km²) was used for urban

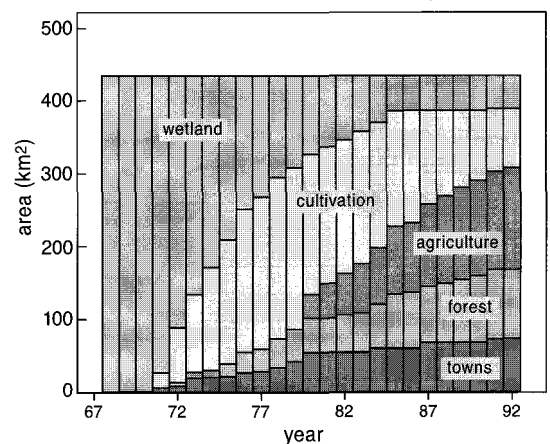


Fig. 1. Development of land use in the polder South Flevoland after embankment and sowing of reed in 1968.

development (Fig. 1).

After reclamation of the Lauwersmeerpolder (1969) from the Waddensea, a fresh water lake ($\pm 20 \text{ km}^2$, i.e. 22%) remained in the lowest central part of the area. The higher sandflats and former salt-marshes fell permanently dry. In this polder no reed was sown and vegetation succession on the former sandflats was slow, due to persisting salinity (Joenje 1978). On the higher parts along the edge of the polder suitable breeding habitat for Marsh Harriers emerged in the first years after embankment (Altenburg *et al.* 1987), due to natural development of dense vegetation, dominated by *Atriplex prostrata*, *Epilobium hirsutum* and reed. After about ten years, reed gradually spread over the former sandflats, thereby extending the potential breeding habitat for Marsh Harriers (Altenburg *et al.* 1987). For a detailed description of vegetation development and management in the Lauwersmeer we refer to Beemster *et al.* (1989). In contrast with South Flevoland, no large-scale cultivation of the major breeding grounds occurred.

The number of Marsh Harrier nests was determined annually in both polders for the first 25 years after reclamation (until 1994). Data on reproductive output were collected in South Flevoland from 1975 to 1987, and in the Lauwersmeer from 1977 to 1994. Nests were located by observing courtship behaviour, nest building and prey deliveries. A clutch was considered completed, when at two consecutive nest visits the same number of eggs was present. Laying date of the first egg was determined by back-calculation, assuming that the eggs were laid every other day. When the nest was found after the laying period we used the wing-length of the eldest nestling to estimate hatching date and subtracted 33 incubation days, to calculate the laying date of the first egg of the clutch (Zijlstra *et al.* 1992). Reproductive success was recorded shortly before fledging, when the young were ringed. Prey items found on the nests were counted and identified.

Common Vole abundance was estimated in the Lauwersmeerpolder for the years 1981 to 1992, by means of break-neck trapping, per-

formed six times per year (1981-1986) and then three times per year (March, July, September, in 1987-1992). At every census, 500 traps, baited with carrot, were distributed over ten fixed plots (50 traps per plot). The traps were checked for the next three days and then removed. This resulted in $500 (\text{traps}) \times 3 (\text{nights}) = 1500 \text{ trapnights}$ per census (for details, see Dijkstra *et al.* 1988). Additional information on local vole densities was available from other sources (Daan & Slopsema 1978, Hoogenboom *et al.* 1984, Masman *et al.* 1988, Dijkstra *et al.* 1990). Mean temperatures per 10-day interval, based on data from the five main meteorological stations in The Netherlands, were derived from the Royal Dutch Meteorological Institute (KNMI). In order to analyse annual variation in reproductive parameters in relation to weather, we used relative temperature, i.e. the difference between the actual temperature and the long-term average value (1961-1990), for the dates concerned. The statistical package used for the analyses was SX (version 4.0, NH Analytical Software Comp. 1992). All tests were two-tailed, unless stated otherwise.

RESULTS

Marsh Harriers in The Netherlands: ringing data

Quantitative data on annual variation in reproductive parameters of Marsh Harriers in The Netherlands are lacking for the first half of the 20th century, but there is some basic information on the number of nestlings ringed. From 1935 until the early 1970s, the annual number of nestlings ringed averaged about 25 (Fig. 2A). Subsequently, the numbers sharply increased to around 500 individuals annually. In total, 8285 nestlings were ringed up until 1990. When eliminating long-term trends, by expressing the annual number ringed as a multiple of the 5-year running mean (Fig. 2B), considerable variation between years remained. In the early years this is obviously related to the small sample sizes, but also in recent years, when consistently more than 300

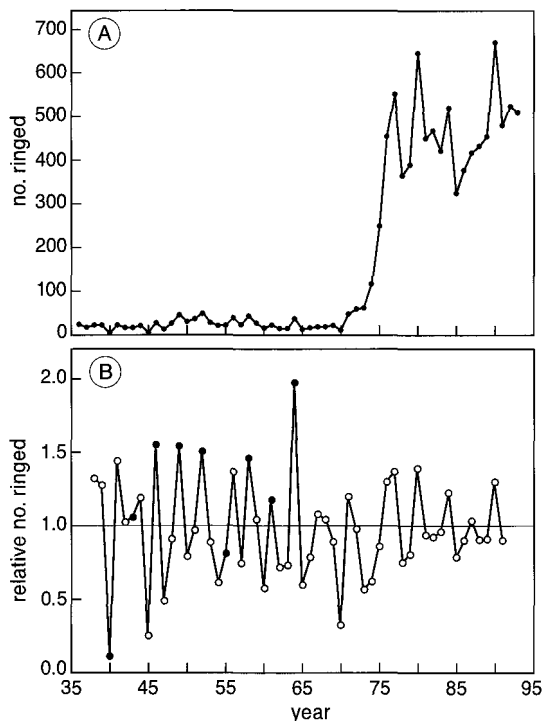


Fig. 2. (A) The annual number of Marsh Harrier nestlings ringed in The Netherlands (1935-1993, source: Vogeltrekstation Heteren). (B) The number ringed, expressed as a multiple of the 5-year running mean. Closed symbols represent vole peak years in The Netherlands, as reported by van Wijngaarden (1957) and Cavé (1968).

nestlings were ringed, the annual figures also varied considerably. Especially during the late 1940s relatively high numbers of Marsh Harriers were ringed during peak vole years (evident country-wide: van Wijngaarden 1957). Potentially, fluctuations in population size, reproductive output (number of nestlings per brood) or ringing intensity may be responsible for the observed variation. While ringing intensity undoubtedly changed over the years, this cannot be quantified. Variations in population size and reproductive success will be analysed here, with special reference to the Marsh Harrier populations in Flevoland and the Lauwersmeerpolder.

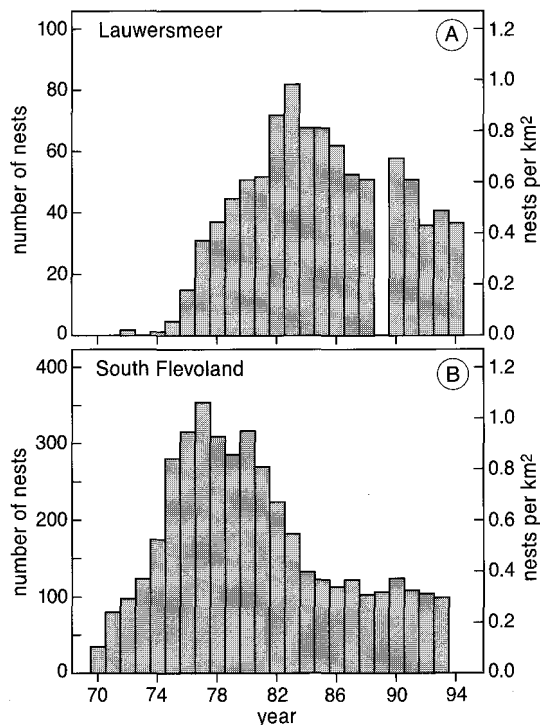


Fig. 3. (A) The number of Marsh Harrier nests in (A): the Lauwersmeer (90 km²) after reclamation in 1969, and (B) South Flevoland (430 km²), reclaimed in 1968.

Fluctuations of the breeding population

Little is known about the number of breeding pairs of Marsh Harriers in The Netherlands in the first half of the century. The first estimate of the total Dutch breeding population was c. 200 pairs in 1940 (Bakker 1954). Before this, estimates are available only for some local populations and restricted time-spans (e.g. van der Ploeg *et al.* 1976), and the total number was probably similar as in 1940. Through rapid colonization of the Noordoostpolder (Bakker & van der Zweep 1949 & 1954), reclaimed in 1940, the Dutch population expanded to 400 pairs in 1950. During the next twenty years the numbers decreased, until 100-150 pairs were left in the late 1960s. This decline has been attributed to the combined effect of persecution and the use of persistent pesticides (Bijleveld 1974, Teixeira 1979). In the 1970s a strong

increase in numbers occurred, to about 1000 pairs in 1980 (SOVON 1987). The population continued to expand in recent years: in 1992, approximately 1400 breeding pairs were estimated for The Netherlands (Bijlsma 1993).

The new polders South Flevoland and the Lauwersmeer, account for a large part of the population expansion (Teixeira 1979, Altenburg *et al.* 1987). The reedbeds in South Flevoland (430 km²) were colonized rapidly, and a maximum of 350 pairs (0.81 pairs km⁻²) was reached in 1977 (Fig. 3B), which was more than half the Dutch population at that time. Although cultivation of the reedbeds was already in full progress by then (see Fig. 1), the numbers declined only since 1981. After 1985 (125 nests), the rate of decline decreased, resulting in about 100 nests in 1993, mainly concentrated in two nature reserves, Oostvaardersplassen and Lepelaarplassen (Fig. 3B).

In the Lauwersmeer it took longer before the area was colonized (Fig. 3A, Altenburg *et al.* 1987). Suitable breeding habitat developed more gradually, because of the high salinity of the soil (Joenje 1978). Peak numbers were reached in 1983 (83 nests; 0.91 pairs km⁻²), 14 years after reclamation. Subsequently the population declined steadily, although no large-scale cultivation has taken place. In 1994, ten years after the peak, there were 38 nesting attempts (Fig. 3A). In 1994 only 10% of the Dutch population was located in South Flevoland and Lauwersmeer, due both to the decline in those areas, and a simultaneous increase in other parts of the country, especially the Wadden Sea islands and the Meuse-Schelde delta (Bijlsma 1993).

Food abundance and predation

New land reclamations are characterized by colonization of a limited number of plant and animal species, with high densities caused by rapid growth and reproduction. Extremely high densities of the Common Vole, one of the most important prey species of wetland raptors (Glutz von Blotzheim *et al.* 1971), are also typical of young polders (Cavé 1968, Dijkstra 1994). In later years vegetation succession is slower and vole 'pla-

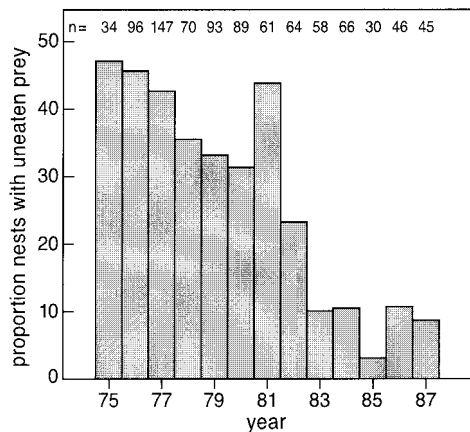


Fig. 4. The percentage of Marsh Harrier broods in Flevoland where fresh, as yet uneaten prey was present at the nest when the nestlings were ringed. This percentage declined in the course of the thirteen years of study: logistic regression: δ deviance = 78.7, $F_{1,11} = 44.65$, $P < 0.0001$. Numbers indicate the number of nests checked.

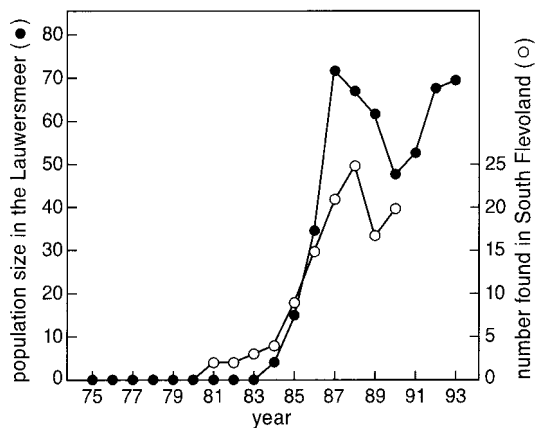


Fig. 5. The number of Red Foxes in the Lauwersmeer (population size) and South Flevoland (the number reported as traffic victims or drowned in canals).

gues' were not recorded anymore in the naturally developing parts of the study areas. Since the Marsh Harrier is not a typical vole specialist, it remains speculative whether the total potential prey abundance for this raptor indeed decreased with

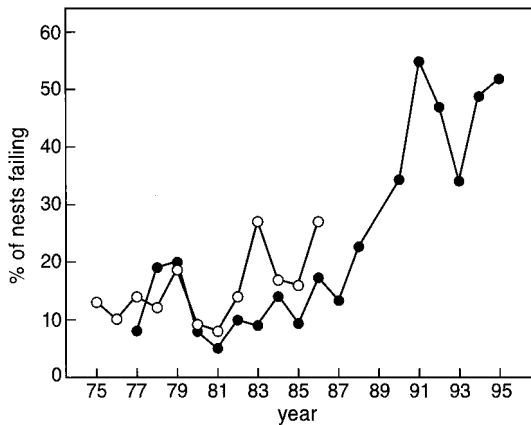


Fig. 6. Annual variation in failure of Marsh Harrier nests in the Lauwersmeer and Flevoland from 1975–1995.

the age of the polders. Prey species may include birds and their eggs, mammals, amphibians and fish (Schipper 1973a, Witkowski 1989, Clarke *et al.* 1993). However, the proportion of nests where fresh, yet uneaten, prey was present when the young were ringed, decreased significantly over the years (Fig. 4), suggesting worsening food conditions.

Foxes colonized the polders during the second decade after embankment (Figs. 5A & B). This species is a competitor for food, and a predator of Marsh Harriers. After the appearance of the fox in the Lauwersmeer, colonies of ground-nesting species, such as gulls disappeared within two years, and the number of breeding ducks and waders decreased considerably (Beemster *et al.* 1989). These species, their eggs and young were regularly preyed upon by Marsh Harriers in the early years after embankment of the polders (Altenburg *et al.* 1987). Furthermore, harrier nests were predated by foxes and occasionally adults were killed. The first foxes were observed in the Lauwersmeer in 1985, after which their numbers rapidly increased (Fig. 5A), while the annual number of Marsh Harrier nesting attempts and nesting success declined (e.g. Fig. 3A, Fig. 6). In the majority of cases there was direct evidence for predation, such as broken eggshells or dead young with

bite wounds. Sometimes predation by a fox was actually observed, and remains of Marsh Harriers were found at fox dens. Especially in the Lauwersmeer, harrier nests were vulnerable to ground predators because the reedbeds are relatively dry. The situation is different in Flevoland, where large inundated reedbeds are present in the two nature reserves. Since 1990, Marsh Harrier nests in these reserves were sited exclusively at inundated spots (pers. obs.).

Parameters of reproductive success

Long-term trends in breeding performance

Figure 7 gives an overview for both study areas of the average clutch size and number of fledglings raised, during the study period. The average clutch size was 4.59 eggs (SD = 1.0, $n = 397$) in

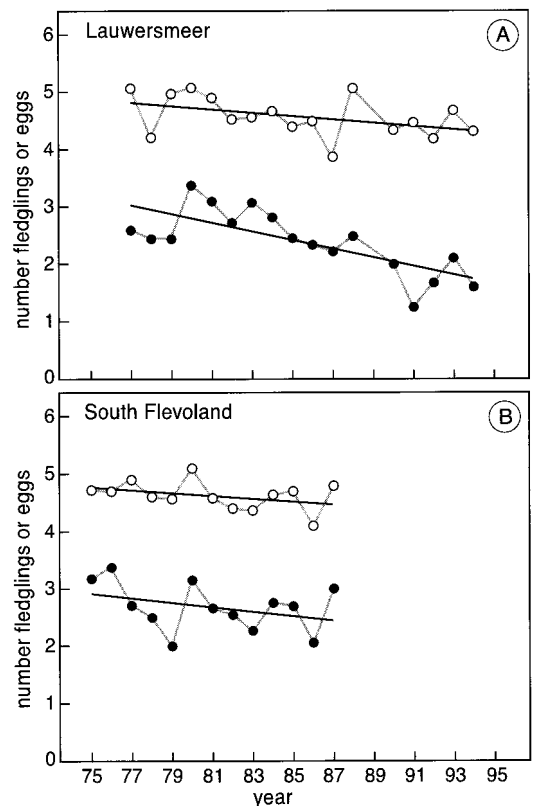


Fig. 7. Annual variation in clutch size and brood size at fledging in (A) the Lauwersmeer, and (B) Flevoland.

the Lauwersmeer, and 4.68 eggs (SD = 0.99, $n = 590$) in Flevoland (Mann-Whitney- U -test, $z = 1.226$, N.S.). The most frequent clutch size was five ($n = 431$, 43.6%, range 2-8). A slight but significant decrease in clutch size of about 0.5 egg occurred over the study period in both polders (Figs. 7A & B, combined data: $\text{clutch size} = -0.024 \times \text{years after embankment} + 6.63$; $n = 987$ clutches, $F_{1,985} = 14.8$, $P < 0.001$). The number of fledglings per successful nest also decreased slightly by about 0.3 fledgling over the study period (combined data: $\text{numbers fledged} = -0.014 \times \text{years after embankment} + 4.30$; $n = 1260$ broods, $F_{1,1258} = 6.12$, $P < 0.05$). The number of fledglings produced per egg in successful nests did not change over the twenty years of study. However, the number of fledglings per nest (including failed nests) decreased significantly, both in the Lauwersmeer (Fig. 7A, $y = -0.08x + 8.96$, $n = 642$, $F_{1,640} = 45.2$, $P < 0.0001$) and in Flevoland (Fig. 7B, $y = -0.04x + 5.62$, $n = 896$, $F_{1,894} = 6.42$, $P < 0.02$). The strongest decline occurred in the Lauwersmeer (difference between slopes: $F_{1,1534} = 4.83$, $P < 0.05$).

Clutch initiation occurred over 81 days, from 23rd March to 14th June ($n = 1385$ nests). Mean laying date in the Lauwersmeer from 1977-1994 was 30th April (day number counted from 1 January: 119.5 ± 11.1 , $n = 553$), and in Flevoland (1975-1988) four days earlier: 115.9 ± 10.7 , $n = 826$, Mann-Whitney- U -test, $z = 5.89$, $P < 0.001$). A similar difference was found in Kestrels *Falco tinnunculus* (Beukeboom *et al.* 1988). Onset of laying became later in the course of the years ($n = 1379$ nests, $F_{1,1376} = 44.9$, $P < 0.001$), in combination with a consistent difference in timing between the study areas throughout the years ($F_{1,1376} = 15.3$, $P < 0.001$).

The clutch size of many single-brooded species declines with laying date (Klomp 1970, Daan *et al.* 1989). In the Marsh Harrier there was a negative relationship both for the annual means of the variables ($\text{annual mean clutch size} = -0.032 \times \text{annual mean laying date} + 8.44$, $n = 20$, $F_{1,18} = 5.3$, $P < 0.05$), and individual values combined over all years and both areas (Fig. 8; $\text{clutch size} =$

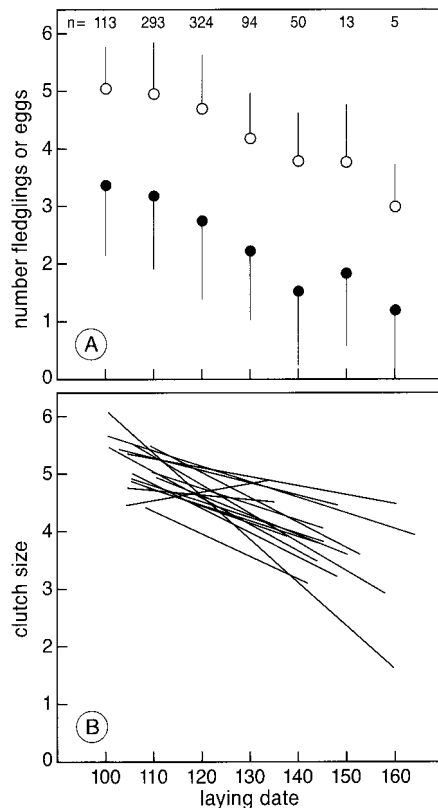


Fig. 8. (A) Mean clutch size \pm SD and brood size at fledging for 10-day clutch initiation intervals (all years and both areas combined). The numbers indicate the number of nests. (B) Linear regressions for individual years of clutch size and laying date, for the Lauwersmeer population.

$0.034 \times \text{laying date} + 8.86$; $n = 903$, $F_{1,901} = 163.9$, $P < 0.001$). This latter relationship differed between years in terms of the intercept (Fig. 8B; $F_{18,883} = 2.01$, $P < 0.01$), but not the slope (year \times laying date interaction: $F_{18,865} = 1.26$, N.S.), and did not differ between Flevoland and Lauwersmeer ($F_{1,882} = 1.32$, N.S.). Apart from laying date, apparently additional year-specific factor(s) impose an effect on the clutch size produced.

Annual fluctuations in breeding performance

Weather conditions influence thermoregulation costs and may also influence the profitability of

Table 1. Annual Common Vole-index, i.e. the average number of Common Voles captured per 100 trapnights in the Lauwersmeerpolder (March, July and September 1981-1992). Peak vole years are indicated with *. Sources: 1: this study, 2: live-trapping (Daan & Slopsema 1978, Hoogenboom *et al.* 1984), 3 & 4: Kestrel vole hunting-yields (Masman *et al.* 1988, Dijkstra *et al.* 1990), 5: Marsh Harrier and Montague's Harrier vole hunting-yields (Beemster & van Rijn 1995).

Year	Vole-index	Peak years	Source
1977	-	*	2, 3
1978	-		2, 3
1979	-		2, 3
1980	-	*	2, 3
1981	3.2		1, 3
1982	4.3		1, 3
1983	6.1	*	1, 3
1984	3.2		1, 3
1985	4.2		1, 4
1986	5.8	*	1, 4
1987	3.1		1
1988	5.3		1
1989	6.5	*	1
1990	6.7	*	1
1991	4.6		1
1992	4.5		1
1993	-	*	5
1994	-		5

hunting behaviour (Rijnsdorp *et al.* 1981, Masman *et al.* 1988). Effects of temperature and rainfall on the reproduction of various species of raptors have been demonstrated (Cavé 1968, Meijer *et al.* 1988, Bijlsma 1993). Since the Dutch Marsh Harrier population is migratory (Dijkstra & Zijlstra 1994), local weather conditions during winter might be irrelevant. The number of days with maximum temperature below zero (frost-days, IJnsen 1991), scored each winter from November through March, had no significant effect on clutch size ($n = 987$ clutches) or laying date ($n = 1385$) of Marsh Harriers during the years 1975-1994.

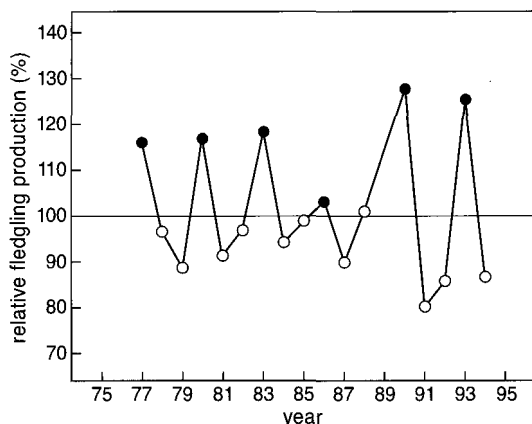


Fig. 9. Annual index of fledgling production of the Lauwersmeer population, expressed as a multiple of the 3-year running mean. (●): vole peak years; (○): other years (see Table 1).

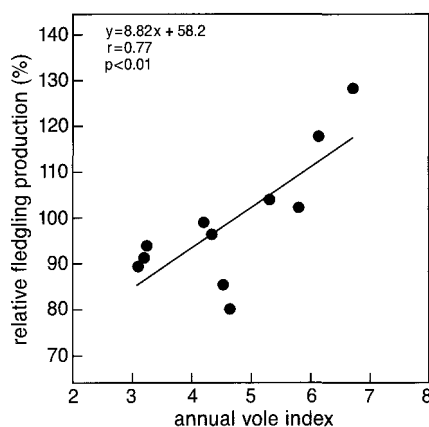


Fig. 10. Annual index of fledgling production of the Lauwersmeer population, expressed as a multiple of the 3-year running mean, as a function of the vole-index (voles trapped per 100 trapnights). The annual vole-index was established by taking the average value of the March, July and September census (4500 trapnights per year).

However, annual mean clutch size was positively correlated with the annual deviation from long-term average temperatures during the (pre)-laying month (21 March-20 April): ($y = 0.09x + 4.51$, $n = 20$, $F_{1,18} = 5.8$, $R^2 = 0.26$, $P < 0.05$). Annual lay-

Table 2. Mean clutch size (\bar{x}), standard deviation (SD) and numbers (n), laying date and fledgling production of Marsh Harriers in the Lauwersmeer (1977-1994), during vole peak years and other years. The relative size of the Marsh Harrier breeding population in any year was calculated by expressing the number of nests as a multiple of the 3-year running mean, thereby controlling for the long-term trend in population size (see Fig. 3). The same method was used to calculate relative fledgling production of the population. Mann-Whitney- U -test.

Reproductive parameters	Peak vole years			other years			P
	\bar{x}	SD	n	\bar{x}	SD	n	
Clutch size	4.74	1.06	137	4.50	0.95	255	< 0.05
Laying date	119.90	11.50	204	119.50	10.80	338	N.S.
no. fledglings per successful nest	3.19	1.01	187	3.02	1.01	298	N.S.
no. fledglings per nest (all nests)	2.55	1.57	234	2.29	1.56	393	< 0.05
Annual relative no. nests	1.07	0.04	6	0.97	0.06	11	< 0.01
Annual relative no. fledglings per nest	1.11	0.09	6	0.95	0.08	11	< 0.01
Annual relative total fledgling production	1.18	0.09	6	0.92	0.07	11	< 0.01

Table 3. Multiple regression analyses of individual clutch size in the Lauwersmeer population. In the analysis given above, two variables were dropped from the model: years after embankment and temperature pre-laying month ($R^2 = 0.20$, $n = 358$). In the analysis given below, laying date was excluded from the model ($R^2 = 0.045$, $n = 392$).

independent variables	coefficient	F	P
individual laying date	-0.036	18.6	< 0.0001
annual vole category	+0.203	5.1	< 0.05
annual vole category	+0.294	7.1	< 0.01
years after embankment	-0.029	10.2	< 0.002
temperature pre-laying month	+0.037	5.9	< 0.02

ing date was negatively associated with temperature during this time of year: ($y = -0.57x + 119.7$, $n = 20$, $F_{1,18} = 6.7$, $R^2 = 0.28$, $P < 0.02$). No significant effect of rainfall (amount and duration) on laying date and clutch size could be detected.

Food abundance has probably declined in our study areas during the twenty five years after embankment (Fig. 4). Superimposed on these long-term changes, are annual differences in prey den-

sity. One of the prey species of Marsh Harriers is the Common Vole. This species exhibits a 3-year population cycle, which is very pronounced at high latitudes (Hansson & Henttonen 1988), and is also detectable in the temperate zone (van Wijngaarden 1957). Using data from the Lauwersmeer vole trapping census, and additional information from other sources, local vole peak years could be defined (Table 1). Clutch sizes during

vole peak years in the Lauwersmeer were significantly larger than in the remaining years (Table 2). However, in spite of the negative association between clutch size and laying date, as shown before, mean laying date in vole peak years was the same as in other years (Table 2). This indicates a direct effect of annual vole abundance on clutch size, independent of laying date. This result is in line with the year-specific relationship between clutch size and laying date (Fig. 8B). Given a certain laying date, the clutch size produced was higher in peak vole years than in the remaining years. Also the number of fledglings per initiated clutch was 0.26 nestlings higher on average in vole peak years (Table 2).

In order to analyse the effect of annual fluctuations in vole abundance on the number of nesting attempts and total fledgling production we corrected for the long term trends in these variables (Figs. 3A & 7A). For each year, the numbers of nesting attempts and fledglings produced were expressed as a multiple of their three year running-mean values. These relative estimates of population size and production were significantly higher in vole peak years (Table 2, Fig. 9). For the twelve years when vole abundance was quantified in the trapping census (1981-1992, see Table 1), the relative annual fledgling production of the total population was positively associated with the vole index (Fig. 10).

Only for the Lauwersmeer vole abundance estimates were available for the years under study, and for this area a multiple regression analysis, explaining variation in clutch size and including all independent variables mentioned thus far, was performed (Table 3). This analysis revealed significant independent effects of laying date (-) and vole abundance (+) on clutch size. The significance of time since embankment (-) and temperature in the pre-laying period (+) on clutch size, was absent when laying date was included in the model. Apparently these factors impose an effect on both clutch size and laying date, and have no date-independent effect on clutch size, in contrast to annual vole abundance.

DISCUSSION

The breeding population of the Marsh Harrier in The Netherlands expanded from 100-150 pairs in the late 1960s to about 1400 pairs in 1992 (Teixeira 1979, Bijlsma 1993). Several factors may have allowed this tenfold increase in roughly twenty years. First, the ban on persistent pesticides in Europe had a positive effect on reproductive output (Opdam *et al.* 1987, Witkowski 1989). These compounds caused direct mortality (Koeleman *et al.* 1969), and, at sub-lethal levels, affected hatchability of the eggs through shell-thinning, resulting in dramatic declines of population size of several raptor species after 1950 (Newton 1979). A second mortality factor was severe human persecution (Bijleveld 1974, Newton 1979). During the 1960s and early 1970s, however, protective legislation of raptors was established in many European countries, including France and Spain where previously many Marsh Harriers were shot on migration (Dijkstra & Zijlstra 1994). Although the laws are still frequently violated, persecution has probably become less severe during the last two decades (McCulloch *et al.* 1992). For the Dutch Marsh Harrier population, a third factor, analysed in this study, was the habitat expansion due to the reclamation of South Flevoland (1968) and the Lauwersmeerpolder (1969).

The South Flevoland population reached a maximum of 350 pairs, ten years after embankment (Fig. 1A). At that time more than 50% of the Dutch population was breeding in the new polders, and the recovery of the population on the traditional breeding grounds was much slower (Teixeira 1979, Bijlsma 1993). A moderate increase also occurred in other W. European countries in the early seventies (Underhill-Day 1984, Jørgensen 1989). The high density of approximately one pair km⁻² indicates the apparent attractiveness for Marsh Harriers of the young polders. Although reproductive performance during the first years of colonization may be relatively low due to settlement of unexperienced, subadult breeders (Altenburg *et al.* 1987), the most favourable circumstances for Marsh Harriers in the pol-

ders probably occurred during the first decade after colonization. During the 1980s the harrier populations in both polders declined considerably. Furthermore, clutch and brood size decreased significantly during the twenty years of study, and laying dates became later. Clutch size was negatively associated with laying date and there is strong evidence that later laying generally reflects poorer conditions (Daan *et al.* 1989). This strengthens the view that breeding conditions deteriorated with the age of the polders. Several factors were probably involved in these long term changes. First, the area of suitable breeding habitat in South Flevoland decreased to only 10% of that available immediately after reclamation. During the 1980s, this probably limited the number of breeding pairs. Simultaneously, food availability was probably reduced, since fresh prey on the nests became increasingly scarce over the years (Fig. 4). This reflects the combined effect of (1) habitat succession accompanied by less pronounced 'outbursts' of prey species such as the Common Vole (Dijkstra 1994), and (2) a reduction of potential hunting habitat for harriers, due to urban development, and growth of forest plantations (Fig. 1). Probably prey abundance was also lower in intensively managed farmlands, compared with the preceding cultivation stage, when trenches with natural vegetation were available, at every ten meters distance. Hunting harriers show strong preference for these elements in arable land (Underhill-Day 1984). In addition to the restriction of breeding habitat and less favourable food circumstances, also nest predation had an increasing negative effect on reproductive success during the 1980s. In both polders the number of foxes rapidly increased, accompanied by an increase in nest predation to 40-50% in the Lauwersmeer. These figures are attributable to the lack of inundated reedbeds, in contrast with the nature reserves Oostvaardersplassen and Lepelaarplassen in South Flevoland. At locations where nests were frequently predated in the Lauwersmeer, the number of nesting attempts dropped considerably (pers. obs.), resulting in a reduction of the local population. Emigration was evidently involved,

because marked breeding birds were occasionally recorded nesting outside the Lauwersmeer in the year after a nest failure, but not after a successful breeding attempt. During the 1990s the annual fledgling production in the Lauwersmeer varied from 1.3 to 2.1 fledglings per initiated clutch. These figures are low compared with the early years of our study and other populations (Bock 1979, Underhill-Day 1984, Jørgensen 1989, Witkowski 1989). In another population suffering high predation pressure, a similar, low production of 1.6 fledglings per nest was found (Bavoux *et al.* 1989).

Superimposed on these changes were annual fluctuations in local Common Vole densities, which had a considerable effect on the number of breeding pairs, as well as on fledgling production. Although the Marsh Harrier is generally regarded as a generalist (Schipper 1973b & 1978, Witkowski 1989), compared to vole specialists like the Kestrel *Falco tinnunculus* and Short-eared Owl *Asio flammeus*, voles were apparently of major importance for the demography of harriers in the young polders. Annual variation in weather also affected Marsh Harrier reproduction: mean annual laying date was negatively correlated with the average temperature during the period from 21st March to 20th April. Clutch size was positively associated with temperature. During this month, most local breeding birds have returned from their wintering grounds, and male-female prey deliveries occur in preparation for laying. Since the average temperature during this month was 5.8°C, and the years under study varied in temperature from 0°C to 13.6°C, there could have been considerable annual variation in thermoregulation costs. The mechanism of this temperature dependence is unknown but the allocation of energy to egg formation is apparently retarded under adverse temperature conditions. In the sedentary Dutch population of the Kestrel, winter severity affects subsequent timing of reproduction and clutch size (Cavé 1968, Meijer *et al.* 1988).

Our results suggest that breeding conditions for Marsh Harriers have been particularly favorable during the period immediately after reclama-

tion of the polders, as soon as suitable breeding habitat had developed. High food abundance and low predation pressure were the main reasons for the high reproductive output in the early years after embankment of the polders. It has been suggested that the general increase of the Marsh Harrier breeding populations was initiated by surplus production in Flevoland during the 1970s (e.g. Teixeira 1979, Meininger 1984, Underhill-Day 1984). However, whether fledgling production in these areas was high enough to explain the initial increase in the local breeding population, and at the same time accounted for increases elsewhere, can only be calculated when annual survival and the age of first breeding are known. These life history parameters were assessed also within the framework of this study (C. Dijkstra unpubl. data). The results indicate that net immigration to the polders has occurred during the first 5-7 years after settlement, whereas substantial emigration of former breeding birds and potential recruits has taken place during the next decade. Frequent nest predation in the Lauwersmeer in recent years caused reduced recruitment, which was insufficient to compensate adult annual mortality (C. Dijkstra unpubl. data). We anticipate that this population will be further reduced. Both, initial immigration and recent emigration of harriers, illustrate adaptive responses to temporal variation in environmental circumstances. Furthermore, natural selection will favor individuals showing preference for inundated nest sites in the presence of ground predators.

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SAMENVATTING

In deze studie werd de temporele variatie in broedprestaties van de Bruine Kiekendief onderzocht in de polders Zuid-Flevoland (drooggelegd in 1968) en de Lauwersmeer (1969). Het aantal broedparen in Flevoland nam snel toe tot een maximum van 350 paren (± 1 paar km^{-2}) in 1977, gevolgd door een sterke afname in de jaren tachtig. Een zelfde verloop trad op in de Lauwersmeer, hoewel de kolonisatie langer op zich liet wachten en de grootste dichtheid later werd bereikt (1983), waarschijnlijk als gevolg van een tragere successie door de zilde uitgangssituatie. In beide studiegebieden namen de gemiddelde legselgrootte en het aantal uitge-

vlogen jongen per nest af, gedurende de twee decennia na de kolonisatie. Drie factoren waren verantwoordelijk voor de afnemende broedprestaties: (1) een sterke reductie van het oppervlak potentieel broedbiotoop, als gevolg van cultivatie in Flevoland, (2) een reductie in het voedselaanbod in de loop der jaren, geïllustreerd door een steeds kleinere fractie nesten waar verse prooi werd aangetroffen, en (3) een toename van predatie van eieren en jongen, vooral als gevolg van kolonisatie door de Vos in de jaren tachtig. Het simultane effect van deze factoren, resulteerde in een sterke reductie van de broedpopulaties van de Bruine Kiekendief in beide polders. In de Oostvaardersplassen en de Lepe-

laarplassen broedt de soort sinds 1990 bijna exclusief in geïnundeerde rietvelden. Deze broedplaatsen zijn relatief veilig voor grondpredatoren en de aantallen broedvogels zijn hier stabiel. In de Lauwersmeer ontbreken grote oppervlaktes geïnundeerd broedbiotoop. Door de intensieve nestpredatie in deze polder ($\pm 50\%$ van de nesten sinds 1990), is het broedsucces zodanig laag dat de lokale populatie zich in de toekomst niet kan handhaven zonder immigratie vanuit gezonde (bron)populaties.

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